

ALIENS UNGULATES AND THE FUTURE OF WESTERN LANDSCAPES

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Hunting the plains and forests of the West is a favorite pastime of mine. Since boyhood I've taken pleasure in the fresh air and open spaces, scenic landscapes, engagement with nature, and of course, the thrill of the hunt. But these days in the field, I'm constantly aware of an insidious menace that threatens the wildlife, habitats, and ecosystems that are the source of so much pleasure. Aliens—in the form of invasive plants—are among us, and they are changing landscapes throughout the American West and beyond. The changes spell trouble for our big game populations and pose many challenges for those who manage wildlife, forests, and rangelands.

How did these infestations of invasive plants get started? How have they managed to spread so widely? Why are they a problem for big game animals? To understand, we must look deep into our nation's history, examine the functioning of ecological systems and processes, and consider how land management activities help or hinder the search for solutions.

The Alien Invasion

As Europeans explored and colonized the globe, they took along plants and animals. For example, dandelions were taken for food;

and English ivy for ornamental purposes. Others, such as cheatgrass, were spread as contaminants in seed grains brought along to develop crops. Many of these exotic plants existed as small populations or failed to establish. Other species, however, have invasively spread and are now disrupting the ecology of vast regions, such as the cheatgrass invasion in the Great Basin. Cheatgrass invasion increases wildfire susceptibility and frequency, resulting in the loss of native species. Where cheatgrass has taken over large areas, forming a monoculture, there are severe declines in biodiversity and loss of habitat for big game animals.

How widespread is this problem? A survey conducted in 1996 revealed at least 17 million acres of federal lands infested by invasive plants, which had more than quadrupled their range from 1985 to 1996. Invasion of natural ecosystems by exotic plants is recognized as one of the major threats

to biodiversity. It also poses a great threat to grazing animals—both wild and domestic—because the invaders replace the very plants that provide nutrition to grazing animals. Almost without exception, invasive plants are bad-tasting (unpalatable) and of inferior nutritional quality.

How do invasive plants get established? They take advantage of the fact that natural ecosystems are disturbance-based. Wildfires, insect attacks, diseases, floods, and wind storms can kill all or part of the existing vegetation in an area. In a natural process called succession, pioneering plants colonize the open ground, and a series of more complex plant communities replace one another over time. In most ecosystems, the earlier stages of succession consist of grasses, forbs (broad-leaved herbaceous plants), and shrubs. These very same plant groups make up the diets of ungulates, the hoofed animals such as deer, elk, and bighorn sheep. These animals, then,



It may seem ironic, but grazing and browsing animals themselves are a form of chronic disturbance. If too much of a plant is eaten too often, then the health of that plant declines, resulting in decreased fitness or death. Decreased fitness means the grazed plant is less able to compete with its non-grazed neighbors for limited soil, water, and nutrients. It may subsequently fail to reproduce or even die and be replaced by unpalatable plants including alien species.

are dependent on episodic disturbance and the resulting regrowth of plant communities for their well-being. Early-successional stages are their source for food. Things can go wrong when alien plants are present, however. Invasion usually occurs after some form of disturbance kills existing vegetation. Invasive plants become established in the open spaces and displace the early-successional food plants favored by ungulates.

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The Role of Herbivory

Herbivory is the act of an animal consuming plants. Wild ungulates, in their search for food, confront a vast array of vegetation.

Much of that vegetation is not consumed, however, because it has low palatability or physical defense mechanisms such as thorns. Palatability is influenced by the chemical composition of the plant. Some species have secondary compounds that not only taste bad, but may detrimentally affect the animal's digestion or be downright poisonous. Structural compounds in some plants make them relatively indigestible. It is interesting that highly aggressive invasive plants often have secondary chemicals, structural compounds, and/or thorns that offer resistance to herbivory. In avoiding such plants, grazing animals give them a competitive edge over more palatable native plants, thus facilitating their invasion, establishment, and dispersal.

What results is a landscape abundant in vegetation, of which only a portion is palatable and consumed by ungulates. A key management principal for maintaining a healthy, biodiverse landscape is to match the amount of forage that animals remove to the productivity of those plants. Two things happen when animal numbers increase beyond the ability of the forage resource to support them. First, the forage plants are physiologically damaged and may die and be replaced by less-palatable and less-nutritious plants, including invaders. The plant community is altered and in most cases, simplified, so that biodiversity declines. Second, the decline in palatable and nutritious forage causes a decline in animal fitness. Animal reproduction may suffer and winter mortality may increase, causing population declines (termed a "density-dependent response.") Here is the take-home message: when herbivory exceeds the ability of forage species to cope, there follows a change in the direction of succession. The result is a simplified plant community dominated by plant species avoided by ungulates and likely to be infested with invasive plants.

Researchers in Utah investigated these relationships by comparing pastures used by mule deer in winter to pastures used by cattle in summer. The pasture browsed by deer in winter contained abundant and vigorous grasses and forbs, but the shrub component was weakened or died as a result of heavy browsing. Conversely, the pasture grazed by cattle during summer supported abundant and vigorous shrubs but few perennial herbaceous plants. Moreover, in the cattle-grazed pasture, researchers clearly saw that the lack of herbaceous plants, brought about by heavy grazing, provided an empty niche easily filled by unpalatable invasive plants. The effect may be more subtle in the case of deer browsing. A decline in

UNGULATES

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the shrub component might be particularly important following wildfire or other disturbance when secondary succession is initiated. As nitrogen fixers, many shrubs play a long-term role in ensuring supplies of nitrogen—a potentially important factor because many invasive species do relatively well in nitrogen-limited environments. Let's look closer at this and other ways in which ungulates can influence the "hospitality" of habitats to invasive plants.

Other Effects of Ungulates

Ungulates influence the nitrogen cycle by changing the quality of litter, which consists of the plant residues left by grasses and forbs going dormant after the growing season and by the shedding of leaves by trees and shrubs. Litter is an important source of nitrogen—return to the soil, as is the deposition of urine and feces by ungulates. The deciduous shrubs most palatable and nutritious to ungulates are the fastest to undergo leaf decomposition, thereby returning nitrogen to the soil quickly. The properties that make them decompose rapidly are the same ones that make them digestible to ungulates. Conifer needles or sagebrush leaves decompose the slowest because the aromatic compounds contained in them inhibit both decomposition and digestion. These relationships can have either a stabilizing or destabilizing influence on the composition and productivity of plant communities. This can be extremely important in ecosystems in the western U.S. where nitrogen is significantly limiting to vegetation. It can compound herbivory effects by allowing invasive plants to take up and immobilize disproportionately more nutrients, thereby limiting opportunities for native plants to establish and thrive. And as previously mentioned, heavy browsing of nitrogen-fixing shrubs in landscapes recovering from wildfire may limit nitrogen availability and thereby increase the risk of non-native plant invasion.

Associated with herbivory effects are animal movements that result in trampling and solifluction, a type of soil creep that happens when waterlogged soil on top of an impermeable layer moves slowly downhill. Trampling, the damage caused by direct hoof impact, may increase runoff and erosion by reducing plant cover, compacting or detaching soil surfaces, redistributing litter, and enlarging bare openings. On steeper slopes in early spring when soils are supersaturated, soil displaced by herbivores may move downhill through plastic flow. Trampling and solifluction, together or separately, create areas of disturbance that are highly inviting

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to invasive plants.

Certain evolutionary adaptations, termed endozoochory and epizoochory, facilitate the dispersal of plant species and the reseeded of heavily grazed areas. Both involve mechanisms for transporting seeds. In endozoochory, seeds ingested by an animal pass through the gut and are deposited 24-48 hours later, encased in fertilizer that promotes rapid growth. Epizoochory is the transport of seeds on the hair or fur coat of animals, often assisted by a seed coating of nature's "Velcro." These ecological mechanisms have positive and important roles in natural ecosystems. But in today's world, where plants hop from one continent to another courtesy of human transportation systems, these dispersal mechanisms can prove detrimental.

Animal-mediated spread of invasive plants is now a common, worldwide phenomenon. Fruits and seeds eaten intentionally or inadvertently by large herbivores may form a substantial part of their diet. By moving seeds away from parent plants, which usually are competitively superior, animal dispersers are likely to increase the probability of seedling survivorship. Because native ungulates and livestock have predictable patterns of habitat selection, animal-dispersed seeds are likely to be spread among environmentally similar sites. Consequently, invasive plants are often deposited in conditions similar to

where invaders have already established. This role of ungulates, in depositing seeds in environments favorable for establishment, can be particularly important for colonization of invasive plants in fragmented landscapes.

Alien invaders may benefit from endozoochory in additional ways. Invasive species with thick seed coats may have enhanced germination as a result of scarification in the gut. In numerous studies, viable seeds of invasive plant species have been recovered from the feces of ungulates. Our knowledge remains uncertain on how important endozoochory is in initiating or increasing invasive plant infestations in natural systems. It may be that the effects of endozoochory on alien seed transport and input to the seed bank are low at large and medium spatial scales, but very important at small scales and for colonization processes. Whereas endozoochory may be significant at small scales, it is likely that epizoochory is an important mode of introducing and spreading invasive plants at several landscape scales. For example, consider that the fleece of a single domestic sheep can carry as many as 8,500 seeds of 85 plant species.

People are Part of the Picture

The influence of wild ungulate herbivory is strongly influenced by human activities. Before Europeans settled in North America,

wild ungulate grazing was characterized by extensive migrations that probably exerted less long-term influence on plant communities. Ungulates approach landscape use by the law of least effort. Val Geist, a professional member of the Boone & Crockett Club, explained in the 1982 volume of *Elk of North America* that animals must obtain necessary resources (nutritious food) with a minimum of effort in order to maximize the derived benefits. And they must do it with a minimum of costly surprises or risks, such as exposure to predators or hunters. The major reason that animals migrated long distance was to access the best quality forage. Ungulates in late spring typically moved to higher elevations following snowmelt to take advantage of the emerging new vegetation. In late fall the opposite occurred, as animals moved downslope to escape deep snows that made forage unavailable. The establishment of cities, roads, farms, energy extraction, recreational areas, and other trappings of civilization has in many cases changed all that. Today, management has significant influences on wild ungulate migrations and subsequent effects on native plant communities. Controlling ungulate density through hunting seasons is a traditional tool of wildlife managers, but managing game animal numbers alone may not sufficiently alter the relative grazing pressure on some plant communities. In much of the western U.S., plant habitats are now patchy and fragmented. Consequently, wild ungulates may concentrate their use on much smaller areas of habitat, increasing the deleterious effects and potential for such habitats to be invaded by non-native plants. Traffic on roads, off-road recreational use, and livestock grazing all affect the distribution of wild ungulates, often in detrimental ways. Research shows that elk are sensitive to all three of these disturbance types. Secondary effects occur to deer, which tend

to move away from habitats occupied by elk. In establishing the numbers of deer and elk that can be supported by an area, managers need to consider human disturbance as well as acres of habitat. Otherwise, some areas may remain unused while other areas are over-utilized and vulnerable to invasion by non-native plants.

I've already explained that most ungulates favor early-successional plant communities as feeding sites. In forests, they prefer a mix of early-successional habitats for foraging and nearby forested habitats for security cover. The near cessation of timber harvest in the western U.S. has created a shortage of early-successional habitats, particularly west of the Cascade Mountains in Oregon and Washington where trees grow rapidly after logging. This shortage of early-successional or transitory habitats causes animals to concentrate their use on available areas, which subsequently may encourage the establishment and increase of invasive species. The large stand-replacing forest fires plaguing the western U.S. do provide lots of early successional habitats. Often, however, security cover is lacking except on the fringes of the burns, and roads are left open to further discourage ungulate use.

The Bottom Line

The upshot of all this is that invasive species are gaining on us and do pose a serious threat to biodiversity and to the animals that outdoor enthusiasts hold dear. Disturbance occurs as natural events on our landscapes; it is necessary for maintaining diverse habitats that provide food and cover for ungulates and a diverse flora and fauna. The chronic disturbance caused by ungulates can interact with episodic disturbance to alter the trajectory of succession. If severe, this alteration may be detrimental to ungulates and to biodiversity overall. The aliens among us take advantage of the

situation. Invasive species readily establish on disturbed sites and out-compete native plants that already are coping with the negative impacts of excessive herbivory.

Fortunately, measures to conserve the native biodiversity of communities and ecosystems are fully compatible with managing for healthy and productive ungulate populations. It's all about balancing uses to enable ecosystems to remain diverse, productive, and resilient to disturbance. Proper control of livestock grazing is essential for maintaining the mix of native species and preventing an influx of aliens into heavily-used sites. The regulated harvest of wild ungulates is a traditional wildlife management tool for controlling wild ungulate populations. It can also be an effective tool for protecting biodiversity, but to realize these broader objectives, consideration must be given to the ecology of disturbance (e.g., prescribed fire, wild fire) and the interactive role that ungulate herbivory plays in shaping the recovering landscape.

The result can be dynamic landscapes rich with an abundance of native plants and animals, including species sought by hunters. Those are the sorts of landscapes I thrive on when afield and wish nothing less for the future generations who will follow in my boot steps. ■

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